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NOTES ON BOVIDAE (MAMMALIA) FROM THE HADAR FORMATION, AND FROM AMADO AND GERARU, ETHIOPIA

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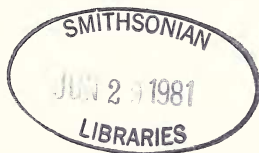
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Abstract

Bovidae are well represented in the Pliocene Hadar Formation, members SH and DD. They comprise two large tragelaphines, one earlier than the other; the bovine *Ugandax* and possibly *Pelorovis* as well; a reduncine common at certain levels and also two rarer reduncines; the hippotragine *Praedamalis deturi*; an alcelaphine possibly allied to *Damalops* of southern Asia and two further alcelaphines; a primitive *Aepyceros*; two or more neotragines; a gazelle, and an ovibovine. Ecologically this is a well-balanced list.

None of the species is identical with any in the Shungura Formation, Omo, Ethiopia. The assemblage is likely to be earlier than those from Members C or upper B of the Shungura Formation.

The Amado bovids could be of the same age as or older than those from the Hadar Formation, although those from Geraru could be younger.



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Introduction

This account is based on fossils collected by the Afar Research Expedition 1973–77. Most of them come from the Hadar Formation on the western side of the Afar Depression at about $11^{\circ}10'N$, $40^{\circ}30'S$ in Ethiopia. The formation consists of about 150–280 m of lacustrine and fluvial deposits in the vicinity of the Awash River and is divided into four members:

Kada Hadar Member (KH) with the tuff (KHT) at its base.

Denen Dora Member (DD), the base of which is marked by the Triple Tuff (TT) band of thin tuffs in a meter-thick bed of green argillite (CC). Above come submembers 1–3.

Sidi Hakoma Member (SH) in which the Sidi Hakoma Tuff (SHT) is succeeded by submembers 1–4.

Basement Member (BM).

A basalt within SH-4 gives a K-Ar date of around 3.0 m.y., and another at a high level in KH a date around 2.6 m.y. Palaeomagnetism is normal except for reversals at the top of SH, including the dated basalt, and the lower part of KH, beneath the dated level. These reversals are identified with the Mammoth and Kaena events within the Gauss normal epoch. The formation appears to have an age spanning 3.3–2.5 m.y. The sedimentary history is thought to show a shallow lake with a wide marginal zone from SHT to DD-1, then the transgression of a large lake with deltaic margins in the rest of DD-1 and 2, then the growth of deltas in DD-3 and KH-1. Further information on geology and dating can be found in Johanson et al. (1978), Taieb et al. (1978), and Taieb and Tiercelin (1979).

Other sites mentioned are:

Kaiso Formation, Uganda, spanning about 5.0–2.5 m.y. and having an earlier and a later faunal level (Cooke and Coryndon 1970).

Karmosit beds, Kenya, probably a little older than 3.4 m.y. (Bishop et al. 1971).

Laetoli, formerly Laetolil, Tanzania. The Laetolil Beds date from 3.59 to 3.77 m.y., and the later Ndolanya Beds are older than 2.4 m.y. (Leakey and Hay 1979).

Langebaanweg, South Africa. The E Quarry assemblage is of latest Miocene or early Pliocene age; the two minor assemblages in Baard's Quarry are younger (Hendey 1976, 1978; Gentry 1980).

Lothagam, Kenya. The Lothagam 1 fauna may be about 5.5 m.y. (Behrensmeyer 1976; Smart 1976).

Lukeino Formation, Kenya, 6.0–6.7 m.y. (Pickford 1978).

Makapansgat Limeworks, South Africa, of Pliocene age (Vrba 1977).

Mpesida Beds, Kenya, about 7.0 m.y. (Bishop et al. 1971).

Mursi Formation, Omo, Ethiopia, where a basalt overlying the fossiliferous levels has been dated to 4.05 m.y. (Butzer and Thurber 1969).

Olduvai Gorge, Tanzania, where Beds I-IV span 2.1-0.6 m.y. (Leakey 1971; Gentry and Gentry 1978).

Shungura Formation, Omo, Ethiopia, with a time span from 4.0 to 0.8 m.y. The upper part of Member B, the lowest level with bovid fossils in appreciable numbers, has an age about 2.9 m.y. and Member G an age slightly younger than 2.0 m.y. (Brown and Shuey 1976: Table 1, Fig. 6; *see also* Drake et al. 1980, Fig. 3).

Sterkfontein Type Site or Main Quarry, South Africa, where most of the mammal fossils come from Member 4, probably dating from between 3.0 and 2.5 m.y. (Vrba 1976, Fig. 20; Partridge 1978).

Two sets of deposits outside Africa are the Tatrot and Pinjor Formations of the Siwaliks Group of India and Pakistan. The first may date from about 4.0 to 2.5 m.y. and the second from 2.5 to perhaps 1.5 m.y. (Pilbeam et al. 1977; Pilbeam et al. 1979; Opdyke et al. 1979).

The following classification of bovids is used (see Gentry 1980:217):

FAMILY BOVIDAE

Subfamily Bovinae

Tribe Tragelaphini Eland, kudu, bushbuck and allies. Mainly browsers in bush, woodland and forest.

Tribe Boselaphini Now represented only by the nilgai and four-horned antelope in India, but formerly occurred in Africa.

Tribe Bovini Cattle and buffaloes, the largest bovids.

Subfamily Cephalophinae

Tribe Cephalophini Duikers, mainly forest antelopes, rarely fossilized.

Subfamily Hippotraginae

Tribe Reduncini Waterbuck, lechwes, kob and reedbucks. Grazing animals found in habitats in the vicinity of water.

Tribe Hippotragini Roan, sable antelope, oryxes and addax.

Subfamily Alcelaphinae

Tribe Alcelaphini Wildebeests, hartebeests, bastard hartebeests. Grazing cursorial antelopes of open country. Also *Aepyceros*, the impala, usually placed in the Antilopini.

Subfamily Antilopinae

Tribe Neotragini Steinboks, dik-dik and allies. Small antelopes found in less dense cover than duikers.

Tribe Antilopini Gazelles, springbok and allies (also *Saiga* and *Pantholops* of Asia). Small-to-medium-sized cursorial antelopes often adapted to conditions of water shortage.

Subfamily Caprinae

Tribe 'Rupicapri' Goral, serow, Rocky Mountain goat. *Rupicapra* might better be placed in the Caprini. Not in Africa.

Tribe Ovibovini Musk ox and takin. Formerly more widespread.

Tribe Caprini Sheep, goats, tahrs.

Specimens are referred to by their field numbers, e.g., AL 116-40, which means specimen number 40 from Afar locality 116.

Horn cores are said to be *obliquely inserted* when their inclinations are low in side view. This is the opposite condition from upright insertions. A *basal pillar* may occur in the center of the medial side of the upper molars or the lateral side of the lower molars, completely or partly separate from the rest of the occlusal surface. It is the entostyle of an upper and ectostylid of a lower molar. The abbreviation *m.y.* denotes millions of years.

I thank Y. Coppens and D. C. Johanson for the invitation to work on the Bovidae from the Afar, and B. T. Gray for much practical help.

Systematics

Tribe TRAGELAPHINI

Tragelaphus aff. *nakuae* Arambourg 1941

This appears to be a fairly common species in DD-2 and 3. The best pieces are:

AL 116-12 DD-3 cranium with much of horn cores

AL 151-2 DD-3 " " " " " "

AL 174-1 DD-2 " " " " " "

The crania agree with *Tragelaphus nakuae*, well known from Members B (units 10 and 11) to H of the Shungura Formation, in overall size (about that of greater kudu, *T. strepsiceros*), in large horn cores with anteroposterior compression and a strong posterolateral keel, and in the braincase roof being almost horizontal in profile and set at a high level. There are differ-

ences, however: the horn cores are more strongly spiralled; the posterolateral keel consequently has a concave, not convex, course immediately above its base; the frontals have a less convex surface between and behind the supraorbital pits; the braincase is longer; and there is no transverse excavation across the skull roof behind the horn core insertions. In the second two of the listed specimens the insertions of the horn cores are more upright and closer together than in *T. nakuae* and the horn cores are less divergent basally than in Shungura Formation examples postdating Member B. In AL 116-12 the insertions are more divergent than in Shungura B and about as oblique as in *T. nakuae* generally.

These characters are mostly more primitive than in *T. nakuae* of Shungura Members C-G. However, the variety of *T. nakuae* occurring in the upper part of Member B does not seem to be a good transitional form and its temporal relationship to the Hadar Formation species is not clear.

The basal pillars on the lower molars of *T. aff. nakuae* are perhaps not so well developed as one would like to see in a putative ancestor of *T. nakuae*.

Tragelaphus aff. nakuae horn cores differ from those of a *Tragelaphus* in the Mursi Formation, which possibly belong to a kudu, by larger size, less outwards curvature as they pass upwards, a stronger posterolateral keel, and an anterior keel which is positioned centrally rather than laterally on the front surface and is perhaps weaker.

Tragelaphus sp. nov.

This species is confined to SH-2 and was evidently replaced after an interval by *Tragelaphus aff. nakuae* in DD-2. The best pieces are:

AL 127-29	SH-2	cranium and much of horn cores
AL 128-9	"	frontlet and horn cores
AL 142-3	"	cranium " " " (Plate 1)

Among the species' distinctive features are long horn cores lacking keels proximally but with an anterior keel and a stronger posterolateral keel distally. The horn cores show a little mediolateral compression at their bases as in *T. strepsiceros*. Compared with *T. aff. nakuae* their insertions are more upright and closer to the orbits, their course is more openly spiralled, and the surface texture is rougher near the base. Other characters are that the braincase roof is more inclined and the temporal ridges weaker than in *T. aff. nakuae*. The anterior tuberosities are very strong on the basioccipital, almost certainly more so than in *T. aff. nakuae*. Basal pillars on the lower molars are probably better developed than in *T. aff. nakuae* but less marked than in Shungura *T. nakuae*. The P₄ hypoconid projects

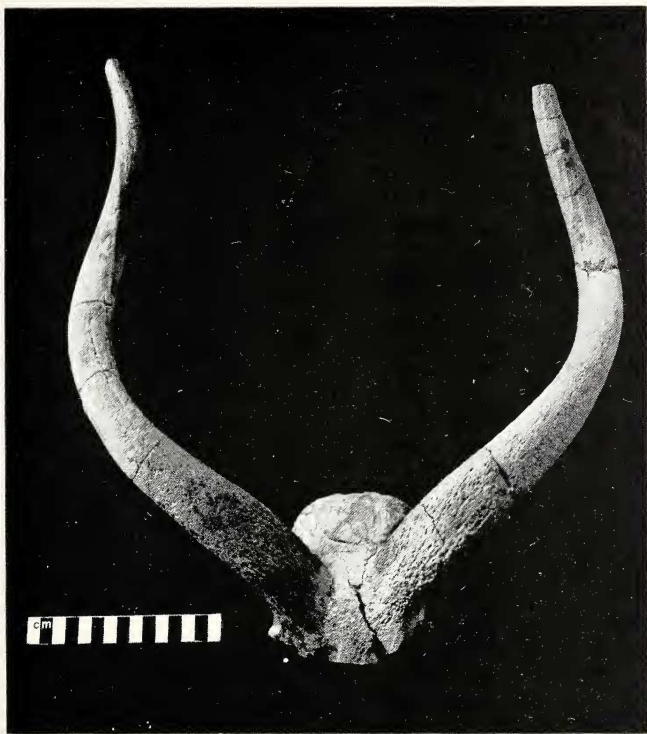


Plate 1. *Tragelaphus* sp. nov. Anterodorsal view of cranium and horn cores, AL 142-3.

strongly and its metaconid is situated relatively posteriorly and well separated from the paraconid, all of which differ from *T. aff. nakuae*.

This species may not be so totally different from other tragelaphines as its horn cores at first sight suggest. It could be a normal archaic tragelaphine, much like an undescribed cranium from the Ndolanya Beds, Laetoli, or like the surviving *T. buxtoni* except in its two specializations of medio-lateral compression and loss of keels on its horn cores. The same two characters later come to be found separately in *T. strepsiceros* and *T. imberbis*, respectively.

Tribe BOVINI

Ugandax sp. nov.

The common bovine of the Hadar Formation is an advanced *Ugandax* represented by several major pieces:

AL 107-1	SH-3	skull with left horn core
AL 116-17	DD-3	cranium with much of horn cores
AL 116-40	DD-3	partial frontlet and horn cores, possibly subadult
AL 127-2	SH-2	cranium with much of horn cores
AL 173-2	DD-2	right horn core and much of frontal
AL 194-1	DD-1	skull with horn cores

Ugandax gautieri, known by the holotype skull (Cooke and Coryndon 1970, Plates 17, 18) from Kaiso Formation deposits of unknown age in the Kazinga Channel, is the type species of *Ugandax* and was thought by Gentry and Gentry (1978:320–322) to be near the ancestry of *Syncerus*. It shares with other primitive bovines its fairly large size; a skull less low and wide than in living bovines; horn cores short-to-moderately long and with almost no compression; braincase short and with a slightly inclined roof; strong temporal ridges; triangular basioccipital; small supraorbital pits and little or no indication of a preorbital fossa. The horn cores show irregular development of keels.

The new species differs from *U. gautieri* by a lower and wider cranium, and by horn cores which are sometimes a little compressed mediolaterally in their lower parts, inserted perhaps further behind the orbits and more widely apart, less backwardly curved in side view, and more divergent. The temporal ridges are wider apart posteriorly, the braincase shorter, anterior tuberosities closer on the basioccipital, and the central longitudinal ridge of the basioccipital less pronounced. It is possible that divergence of the horn cores is stronger and the median vertical occipital ridge better developed in the DD examples, and there is also a good deal of variation not obviously related to the stratigraphic succession.

It is *Syncerus* and not *Ugandax* which occurs in the Shungura Formation. Horn cores of *S. ?acoelotus*, mostly from Member C, emerge nearly transversely from the skull and scarcely pass at all backwards. They have a flattened dorsal surface. An immature skull from Member B unit 12 has horn cores still passing backwards but with greater basal divergence than the Hadar horn cores.

As far as tooth characters are concerned, two of the bovine P₄s (that on the left mandible, AL 116-35 DD-3, and another left one, AL 182-72 DD-2) look more primitive than in bovines from the upper part of Member B of

the Shungura Formation in that the metaconid is aligned more diagonally and less transversely. Others (four from DD-2, one from DD-3, and one from SH-2) look as advanced as in Shungura Member B. The single bovine mandible, 1936A, from the Sterkfontein Type Site (Vrba 1976:47, Plate 26B) has an unerupted P_4 which again compares well with Shungura Member B and the majority of Hadar Formation examples.

A left mandible, AL 165-10 from SH-2, looks more primitive than other Hadar Formation Bovini. It retains P_4 - M_2 , most of M_3 and sockets for P_2 and P_3 and is in early middle wear. It appears primitive in the lack of localized constrictions of the lateral lobes of the lower molars and in the poorly localized ribs on the medial walls of the molars between the stylids. These features resemble *Parabos*, a primitive bovine of the European pre-Villafranchian Pliocene. Other pieces from SH-2 do not look so primitive, but it may still be noted that *Parabos*-like dentitions do not occur in higher members of the Hadar Formation.

?Pelorovis sp.

A piece of horn core, AL 114-1C from DD-2, is about 220 mm long and looks as if it could belong to *Pelorovis* (long-horned buffaloes of the Plio-Pleistocene) or to the older and possibly ancestral *Simatherium*. It is curved in one plane, has no keels, and is compressed, the greatest diameter at its lower end being 72 mm and the diameter at 90° to that one being 57 mm. Remains of an internal sinus at the thicker end suggest that the horn core may be largely complete and may have had a total length scarcely more than 300 mm. It is too incomplete for its insertion position on the skull to be ascertained and its identification must remain tentative.

Tribe REDUNCINI

Kobus sp. A

In the Hadar Formation Reduncini first appear in SH-3 and are mostly found in submember DD-2. They continue in DD-3 but there they constitute a lower proportion of the whole bovid fauna. There are some crania, e.g., AL 157-4 DD-3, and numerous horn cores. Their size is about that of a kob. The horn cores are long and are compressed anterolaterally to posteromedially. They have no keels and poor-to-absent transverse ridges. Their divergence is quite strong and increases toward the tips; they have little or no backward curvature, are inserted fairly uprightly and may even curve forward from base to tip. Temporal lines on the cranial roof are not prominent and approach closely posteriorly. The occipital surface is rather

flat, faces wholly backwards, and is without a smoothly rounded edge; its sides may even be concave upwards. Narrow mastoids lie within the boundaries of the occipital surface, the auditory bulla is inflated but not large, and the braincase is wide rather than high.

There is some puzzling variation in horn core morphology, best exemplified by the pair AL 155-7H from DD-2. They are not quite so long as others; their compression is less clearly anterolateral to posteromedial and more nearly lateral to medial; there is more of a posterolateral keel; divergence is perhaps less and does not increase so much toward the tips; and forward or upward curvature is more distal. Three more specimens agree in these characters and it is doubtful whether they are a separate species from the 14 or so others. Probably they are not.

The Hadar horn cores seem close to a species from Member B units 10 and 11 of the Shungura Formation. This also shows long horn cores with a degree of anteroposterior compression, increasing divergence distally, and little or no backward curvature. However, the Hadar species has anterolateral to posteromedial rather than anterior to posterior compression of the horn cores; the braincase roof is more inclined in profile and the occipital edge less rounded.

An interesting feature of reduncine teeth from the Hadar Formation is that the paraconid on P₄ extends backwards, grows very close to the metaconid and perhaps even fuses with it (Fig. 1). This state cannot be found in other Plio-Pleistocene Reduncini, including those of the Siwaliks or Shungura upper Member B. Something similar can be seen in extant *Redunca arundinum*, but here it is forward growth of the metaconid which may be more important in bringing the two cusps together. It may also be noted that the premolars of Hadar reduncines form a longer row than in extant forms and the molar teeth are less high crowned.

Kobus sp. B

Another reduncine species is represented by a pair of horn cores AL 208-8 from SH-3. They are quite short, a little compressed, with a flattened area on the lateral surface, strong transverse ridges, strong backward curvature, and poor divergence which lessens distally. This species is earlier than nearly all the *Kobus* sp. A in the Hadar Formation. Either it became extinct, at least locally, or it may have been related to the persistent but ever-changing lineage leading to the extant kob.

Kobus sp. C

AL 130-2, possibly from SH, is the proximal part of a horn core with part of the frontal. It is not unlike *Kobus porrecticornis* (Lydekker 1878), a

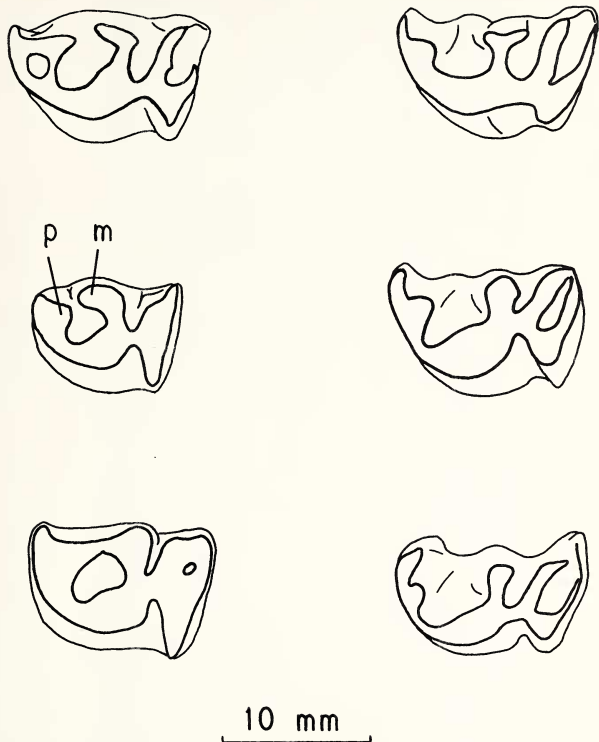


Fig. 1. Reduncini P₄s, all shown as of the left side and with the anterior side toward the left of the figure. Left column, from the top: Hadar Formation, AL 153-3 DD-2, early middle wear; AL 167-5 DD-2, middle wear; AL 156-1A (reversed) DD-3, late middle wear. Right column: Shungura Formation, L 2-46B Member B, early middle wear; F161-39 (reversed) Member H, middle wear; F256-18 Member H, early middle wear. Paraconid (*p*) and metaconid (*m*) approach more closely in the Hadar examples.

small, kob-like reduncine from the upper part of the Dhok Pathan and/or the Tatrot Formation of the Siwaliks, the Mpesida Beds (H. Thomas, personal communication, 1977), Lukeino Formation and Baard's Quarry at Langebaanweg (Gentry 1980: 321-323). This horn core, however, has transverse ridges, hardly any backward curvature (probably less than in *K*.

porrecticornis), was probably inserted more widely from its partner of the other side, and the supraorbital foramen is small (unless what is preserved is only the rearmost of a line of foramina).

Tribe HIPPOTRAGINI

Praedamalis deturi Dietrich 1950

Two horn cores, seemingly of this species, are known from the Hadar Formation:

- | | | |
|-----------|-----------|---|
| AL 188-4 | DD-2 or 3 | much of a nearly straight left horn core with part of the orbit (Plate 2) |
| AL 154-11 | DD-3 | basal part of a horn core |

This species was described from Laetoli by Dietrich (1950:30, Plate 2, Fig. 23) and discussed by Gentry and Gentry (1978:351) who referred it to the Hippotragini. It occurs in the Laetoli Beds at Laetoli according to collections made by M. D. Leakey since 1974. No teeth from the Hadar Formation look hippotragine.

Tribe ALCELAPHINI

?Damalops sp.

Among the best preserved remains are:

- | | | |
|-----------|------|--|
| AL 208-7 | SH-3 | most of skull with horn cores |
| AL 310-18 | — | cranium with base of right horn core |
| AL 353-3 | SH-2 | cranium with much of left horn core |
| AL 161-5 | DD-3 | cranium with partial base of left horn core |
| AL 320-1 | DD-3 | part of cranium, pieces of horn core, cervical vertebrae |

- | | | |
|----------|------|---|
| AL 120-2 | DD-3 | horn cores and much of an associated skeleton |
|----------|------|---|

There are also a large number of horn cores. The absence of face lengthening and of extreme braincase shortening, and the presence of large preorbital fossae are different from extant alcelaphines.

Most of the horn cores are from DD-2 and 3 and show fairly upright insertions, curvature that is upward and forward from the base, divergence gradually increasing from the base, often a swollen basal area reminiscent of *Connochaetes*, and a cross-sectional shape that is squared off posteromedially at the base. The horn cores on the earlier skull AL 208-7 are less curved and less divergent. Moreover, their divergence does not increase continuously but changes fairly sharply at a point about one third of the distance above the base. Other horn cores from SH are curved, however,

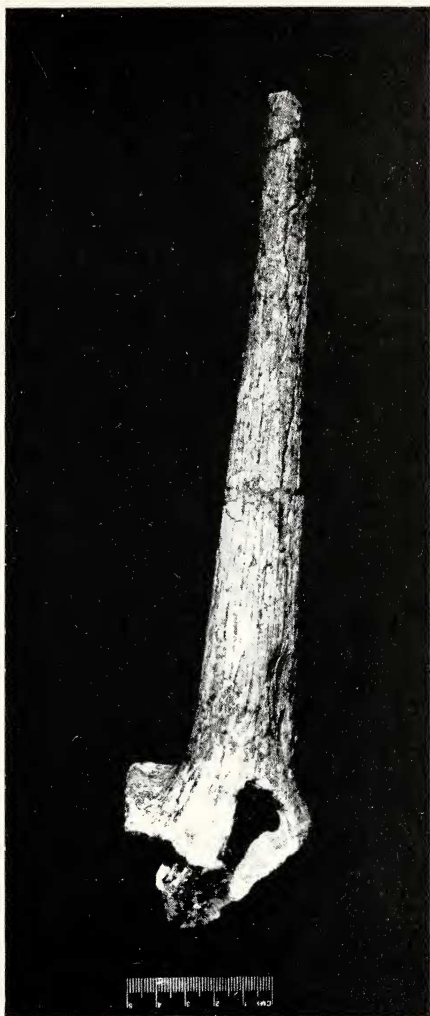


Plate 2. *Praedamalis deturi*. Anterior view of left horn core, AL 188-4.

and it can only be noted that no relatively straight horn cores occur above SH. Possible evolutionary changes may be seen at the back of the skull. In AL 208-7 and AL 353-3 from SH the junction between the base of the nuchal crest and the back of the zygomatic arch is placed rather anteriorly, and each half of the occipital surface faces partly laterally as well as backwards. In the stratigraphically higher cranium AL 161-5 and in AL 310-18 the junction of nuchal crest and zygomatic is more posterior and the occipital surface faces more wholly backwards.

Alcelaphine teeth of the Hadar Formation are probably less hypsodont than in living species; on the upper molars the central cavities are less complicated, the ribs less prominent in relation to the styles, and the medial lobes perhaps less rounded. On lower molars the central cavities are less curved and the medial walls perhaps less outbowed. The rear part of P_4 (hypoconid, entoconid, and entostylid) is less reduced, and the valley between the entoconid and entostylid is perhaps oriented more transversely to the line of the jaw. These primitive features are less clear in relation to alcelaphines of the Shungura Formation and Olduvai Beds I-IV.

It is difficult to classify the Hadar alcelaphine. Compared with *Parmularius* sp. in the Laetolil Beds (Gentry and Gentry 1978:382, Plates 21, 22, Fig. 2) it is larger and its horn cores show distal divergence but not backward curvature. It could be conspecific or closely related to a partial cranium 1959.233 (Gentry and Gentry 1978, Plate 22, Fig. 1) from the Laetolil or Ndolanya Beds, and it could at the same time be a close relative of *Damalops palaeindicus* (Falconer 1859) from the Pinjor Formation and Tadzhikistan, USSR (Dmitrieva 1977). This is on the basis of such similarities as: overall size (about that of extant *Alcelaphus*); high and narrow skull; horn cores inserted closely and not very uprightly above the backs of the orbits, nearly parallel proximally but increasingly divergent distally; frontals raised between the horn bases but not tremendously so; braincase rather long by comparison with presumed later alcelaphines; braincase roof inclined and with little sign of a parietal boss; preorbital fossa large; nasals pronouncedly narrow as a ridge between the preorbital fossae; and a deep face. However, *D. palaeindicus* shows backward curvature of its horn cores, horn cores not tapering rapidly above the base, sides of the braincase parallel and not widening posteriorly, and probably also longer horn cores, shorter braincase, and a tooth row positioned more anteriorly. P_2 is absent on the only two Hadar specimens (both in middle wear) on which its state is determinable, and this contrasts with its presence on a single *D. palaeindicus*.

Alcelaphini sp. 2

A separate smaller alcelaphine species is represented by a badly preserved cranium with left horn core AL 146-1 SH-2. This is like the *Parmularius* sp. from the Laetolil Beds, but it differs in stronger mediolateral compression and more oblique insertions of its horn cores, less of a *Parmularius*-like boss on its cranial roof, a wider braincase and basioccipital, and a nuchal crest which is not concave upwards.

Alcelaphini sp. 3

AL 209-1 from SH-3 is a problematical lower part of an alcelaphine horn core which is not complete enough to be oriented. It curves in one plane and is compressed in the plane at 90° to this plane. Its shape is somewhat like a Geraru species represented by AL 94-1, but it lacks the deep longitudinal grooving of that species.

Aepyceros sp.

Aepyceros is well represented in SH and is proportionately more common there than in DD. There are also two horn cores and a tooth in BM. The best pieces are:

AL 127-3	SH-2	most of left horn core but with much of the pedicel eroded
AL 173-7	DD-2 or 3	much of left horn core, pedicel, dorsal orbital rim and part of left frontal
AL 132-2	SH-1	right maxilla with P ⁴ -M ³ in early middle wear
AL 199-6	SH-1	right mandible with P ₄ -M ₃ in early middle wear

Horn cores in SH differ from *Aepyceros* of the Shungura Formation by their smaller size and by being shorter, less curved backwards and less lyrated, all these features being apparently primitive. Lyrations may be slightly stronger in DD horn cores, i.e., divergence may be greater just above the base (but without equalling that of Shungura examples), but DD horn cores are less complete and the horn core AL 142-4 from SH-2 is not different from those in DD. Two DD horn cores have postcornual fossae smaller than in a single SH example.

The SH horn cores differ from some in the Mursi Formation, Omo, by being slightly smaller, having stronger transverse ridges, less backwards curvature (chiefly shown by the distal parts being recurved upwards), and

less accentuated posterior grooving. The DD ones also differ by their enhanced liration so far as it is a valid character.

The two horn cores from BM, AL 124-21 and -40, the latter being without its basal part, may derive from the same individual. They are perhaps more mediolaterally compressed than SH specimens, and total curvature (backward curvature plus reduction in divergence distally) is probably less. Indeed, they might not have been regarded as *Aepyceros* at all had not internal sinuses been visible low in the pedicel of AL 124-21. The postcoronal fossa of AL 124-21 is larger than in DD specimens.

The upper cheek teeth of Hadar Formation *Aepyceros* have better styles than in the Shungura *Aepyceros* and this is best seen with the mesostyles of the molars. P₄ has less frequent paraconid-metaconid fusion and dP₄ has at least a rear basal pillar.

A proximal femur, AL 122-8 DD-2, is probably of *Aepyceros*. It is interesting in that the lateral parts of the articular head are somewhat narrow anteroposteriorly and the notch between articular head and great trochanter is not very deeply excavated, i.e., it is less distinctive overall than the same bone in extant *Aepyceros*.

Tribe NEOTRAGINI

Madoqua ?avifluminis Dietrich 1950

Neotragini are rare in the Hadar Formation. A right horn core, AL 55-25 from KHT, appears to be more akin to *Madoqua ?avifluminis* from the Ndolanya Beds than to *M. avifluminis* itself which is from the Laetoli Beds.

?Raphicerus sp.

Some neotragine dental remains are too large for *Madoqua*. Several pieces, perhaps from SH-1, belong to a species about the size of extant *Raphicerus* or *Dorcatragus*. An upper molar among them is low-crowned for a neotragine. An M² and M³ in a right maxilla, AL 167-6 DD-2, are similarly low-crowned but perhaps smaller. A mandible, AL 269-2 DD-3, has rather worn teeth. The molars on the mandibles have basal pillars.

?Neotragini sp. indet.

AL 211-2 from SH-4 or DD-1 is a left M³ in early wear which is larger than the teeth just discussed but smaller than Antilopini in the Hadar Formation. It is not very hypsodont and has a strong anterior rib. It agrees with

extant *Ourebia* except in its larger size and the prominence of its metastyle lower down. It differs from the tooth of a small reduncine, YS 4-12, in the Mursi Formation by its larger size and weaker styles.

Tribe ANTILOPINI

Gazella sp.

An unnumbered horn core from AL 333 in DD-2 or 3 is probably from the right side of a *Gazella*. The pedicel is missing and it is incomplete at the tip. Its total length might have been about 130 mm, which is rather short for a gazelle. It has strong mediolateral compression, less backward curvature than Shungura Formation gazelles, and the level of greatest transverse width of cross section is sited nearly centrally as in both Shungura and Olduvai fossil gazelles.

Some dental remains are too small to fit *Aepyceros*. Among them is AL 127-1 SH-1, a left maxilla with P³-M¹ on which the P⁴ has a rib between the styles (albeit less pronounced than the rib on P³).

Some antilopine limb bone parts from AL 132 in SH-1 include an interesting metacarpal AL 132-10. This has a posterior surface more hollowed proximally than at the present day, and it is neither shorter nor thicker than in extant gazelles (Fig. 2). It therefore contrasts with *Antidorcas* from Olduvai Gorge (Gentry and Gentry 1978:430, Fig. 33).

Tribe OVIBOVINI

Ovibovini sp. aff. "*Bos*" *makapaani* Broom

A single skull, AL 136-5 (Plates 3 and 4) from the middle or upper Hadar Formation, with horn cores, cranium, much of the face and the left M³ in middle wear, is of an ovibovine. Among its chief features are that the large but probably short horn cores are compressed posterodorsally to antero-ventrally and emerge transversely from very elevated frontals; the short braincase has a steep roof; and the basioccipital is triangular, has a central longitudinal groove which does not widen posteriorly, and has anterior tuberosities with long, sharp ridges converging anteriorly.

Ovibovine horn cores or teeth are known in Africa as late as the early Pleistocene (Gentry 1978:561). The best known species is *Makapania broomi* Wells and Cooke (1956) from Makapansgat Limeworks and probably from Sterkfontein Type site (teeth which Vrba [1976:48] referred to *M. cf. broomi*), which Gentry (1970) held to be related to *Megalovis latifrons* of the later Villafranchian of Europe. The Hadar form is like *Maka-*

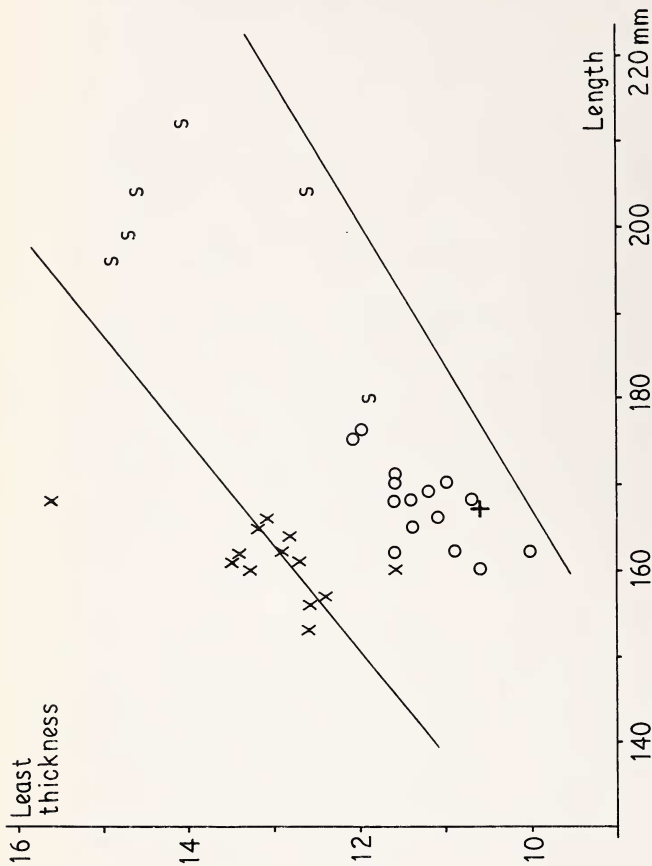


Fig. 2. Length and least mediolateral shaft thickness of metacarpals of some Antilopini. X = *Antidorcas recki*, left sides, from site FLKN, Bed I Olduvai Gorge; S = extant springbok, *A. marsupialis*; O = extant *Gazella thomsoni*; + = Hadar Formation left metacarpal AL 132-10. The upper diagonal line is that along which least thickness is 8 percent of length; the lower line is for 6 percent.

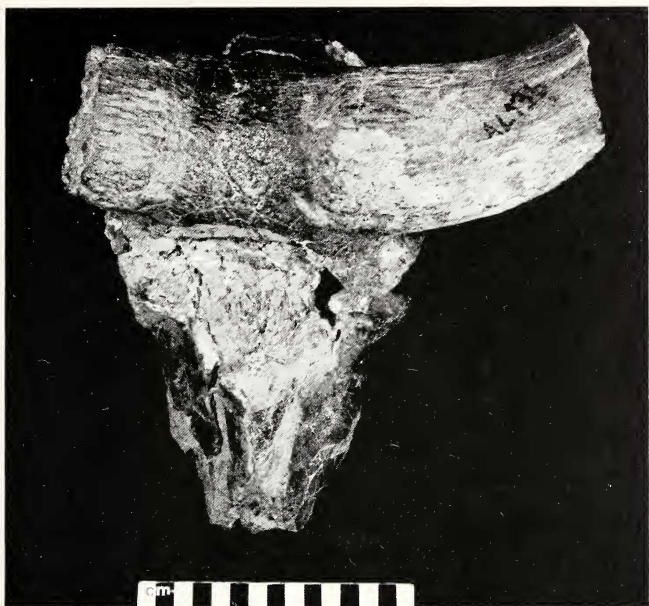


Plate 3. *Ovibovini* sp. aff. "*Bos*" *makapaani*. Dorsal view of skull and horn cores, AL 136-5.

pania broomi in the course and wide divergence of its horn cores and in its projecting orbital rims, but differs in that its horn cores are more massive and probably shorter; their compression becomes more dorsoventral immediately above the base instead of disappearing; the frontals rise much higher so that the cranial roof is very inclined; the anterior part of the zygomatic arch is thicker below the orbits; and the longitudinal groove of the basioccipital persists further anteriorly and does not widen posteriorly.

The Hadar ovibovine is actually much more similar to "*Bos*" *makapaani* Broom (1937) from deposits of unknown age in Buffalo Cave (Cooke 1952:33) near Makapansgat. It is known by a frontlet and horn cores and has never been adequately described. It appears to differ from the Hadar ovibovine only in being slightly smaller and having more compression of its horn cores.



Plate 4. Oribovini sp. aff. "*Bos*" *makapaani*. Lateral view of skull and horn cores, AL 136-5.

At present it looks as if two distinct lineages of ovibovine, have been present in Africa, these being the Hadar Formation and Buffalo Cave stock on the one hand and *Makapania broomi* on the other.

Bovidae from Amado

Bovids have come from three localities at Amado. The first locality, AL 100, has the most bones and six species are represented.

AL 100

A frontlet, teeth and postcranial remains belong to a species smaller than the *Tragelaphus* aff. *nakuae* of the Hadar Formation. The horn cores on the frontlet are long, anteroposteriorly compressed about as much as in Pliocene or Miocene *Tragelaphus*, strongly curved in a lyrate course, having the posterolateral keel better marked than the anterior keel, and inserted above the back of the orbits. They are very like a somewhat larger, as yet undescribed *Tragelaphus* from the Ndolanya Beds at Laetoli. There is some resemblance of both these forms to *T. buxtoni* of the Ethiopian highlands, probably because the latter is a relict species with some primitive characters. The teeth are about the size of the extinct kudu *T. gaudryi* in the Shungura Formation, although the premolars may have been slightly larger. On P₄ the paraconid and metaconid approach but do not join together. A bovine species is represented by some rather low crowned, mostly upper, teeth. A right metatarsal and perhaps a few other postcranial bones can also be identified as bovine. Two alcelaphine teeth appear to come from different-sized species. Four pieces of *Aepyceros* horn cores differ from those in the Hadar Formation by being larger, probably longer, with stronger lyration and with better-marked transverse ridges. They look like *Aepyceros* from the Shungura Formation. A dozen or more teeth, which are probably conspecific with the horn cores, are larger than *Aepyceros* teeth from either the Hadar or Shungura Formations and are probably less high crowned than in the Shungura Formation. Three postcranial bones may also belong to *Aepyceros*. A left upper molar in early middle wear and an unassociated astragalus could belong to the Antilopini.

AL 99

From a second locality, AL 99, come two pieces of mandible, probably from the same individual, with tragelaphine teeth about the size of the species at AL 100, and one or two postcranial bones which could be of the same species.

Two horn cores, a left and a better-preserved right, belong to a small reduncine, apparently *Kobus porrecticornis* (see under *Kobus* sp. 3). A complete and a fragmentary alcelaphine mandible represent a smaller and a larger species as at AL 100. Two horn cores, probably from the same individual, belong to *Gazella janenschi*. They have a slight flattening of the lateral surface and are not closer either to the pattern seen in examples from the Laetolil or Ndolanya beds at Laetoli.

Two pieces of a single medium-sized horn core, AL 99-6, are distinctive but unidentified. The horn core is compressed, perhaps from side-to-side, and curves, perhaps backwards. It is also a little curved along an axis at right angles to the main curvature. There are no keels or transverse ridges but there is a noticeable groove along its most convex edge. There was a sinus in its pedicel. The insertion position was unknown.

AL 104

Only two bovids come from the last Amado locality, AL 104. A large tragelaphine is represented by a frontlet, a mandible, and possibly a scapula. The frontlet is most similar to the cranium AL 116-12 of *Tragelaphus* aff. *nakuae* from the Hadar Formation. This species is larger than the tragelaphine at AL 100. What is presumably a bovine is represented by the stem of a large scapula.

Bovidae from Geraru

Bovid fossils from Geraru were available from localities AL 70, 72, 73, 83, 86, 87, 88, 90, 92, and 94. The main pieces are as follows:

Tragelaphus nakuae

This is represented by a left horn core AL 83-2. It best resembles fossils of this species from Shungura Formation Members C to F. A right M_3 and probably an astragalus are also tragelaphine and perhaps of this species.

Syncerus sp.

This is represented by a damaged partial cranium AL 70-6 with strongly divergent horn cores which are compressed in the dorsoventral rather than the mediolateral plane. Both characters suggest *Syncerus* rather than *Ugandax*. A left maxilla of a bovine comes from the same locality.

?Hippotragini sp.

A left M_3 AL 70-5 may be of a hippotragine, larger than reduncine teeth from Geraru and low crowned compared with teeth of extant hippotragines.

Reduncini

Reduncini are represented by a number of teeth, perhaps slightly larger and more hypsodont than in the Hadar Formation. A short right horn core, AL 74-7, is somewhat like *Kobus subdolos* of Langebaanweg (Gentry 1980) but the teeth are not. One or two postcranial bones are rather doubtfully taken as reduncine.

Alcelaphini spp.

AL 83-4 is a much-damaged horn core possibly of the left side. It is somewhat like the horn cores of the small primitive *Parmularius* from the Laetoli Beds (Gentry and Gentry 1978:382, Plates 21, 22, Fig. 2) or the horn core L 292-29 from Member C of the Shungura Formation which may belong to *Parmularius* or to the *Damaliscus niro* lineages.

Alcelaphine teeth of two different sizes are known from several Geraru sites and must represent different species. In addition there is a right M_3 in middle wear, AL 87-1, with occlusal length 22.3, which is a little smaller again and may belong to a third species. It is a little larger than the Hadar or Amado *Aepyceros*, and differs by having central cavities with more of a typically alcelaphine outline, medial walls with well-rounded lobes, and lateral lobes which are not very pointed.

Bases of two *Aepyceros* horn cores agree in size and morphology with Amado rather than Hadar Formation examples.

A distinctive species, possibly alcelaphine, is represented by parts of left and right horn cores and a separate partial cranium, AL 94-1. The left horn core is long, anteroposteriorly compressed basally, with transverse ridges, inserted above the back of the orbits and close to the midline of the frontals, strongly divergent in its central part but without backward curvature, with irregular but deep longitudinal grooves mainly on the lower part of the medial side, and having sinuses within the frontals and a large one in the horn pedicel. The frontals between the horn core bases are at a higher level than the dorsal part of the orbital rims. The braincase was probably short; its roof is inclined. The temporal lines approach fairly closely at the back of the braincase roof. The occipital surface is rather low and wide with a strong median vertical ridge leaving each half facing partly laterally as well as backwards. The sulci on the internal wall of the braincase appear more similar to four Shungura examples of *Kobus* and *Menelikia* than to alcelaphines, yet the occipital surface is more like alcelaphines than a reduncine. The close insertions of the horn cores are unlike *Connochaetes* or *Oreonagor* (Thomas 1884, Plate 7, Fig. 1), but *Beatragus* could be related. Another possible relationship is to *Makapania*, already mentioned in the account of the Hadar ovibovine. The basal compression and course of the horn cores

as well as their insertion position are all similar. The transverse ridges distally and the longitudinal grooving basally are different, however.

Discussion

The species list for bovids of the Hadar Formation is given in Table I. It is a well-balanced list in which nearly all tribes of bovids are represented. Such a list can be compared with present-day African faunas. The first two entries are successive large tragelaphines that might correspond ecologically to kudu (*Tragelaphus strepsiceros* or *imberbis*) or nyala (*T. angasi*). Two bovines were present as was also usual into the Pleistocene, and the *Pelorovis* was the rarer of the two as in the Shungura Formation. A larger reduncine and a rare smaller one may have had differing ecologies like waterbuck and kob or like lechwe and reedbuck. A hippotragine would correspond to *Hippotragus* or *Oryx*. A larger and a smaller alcelaphine

TABLE I
Species List for Bovids of the Hadar Formation

	SH	DD	Other
<i>Tragelaphus</i> aff. <i>nakuae</i>		X	
? <i>Tragelaphus</i> sp.nov.	X		
<i>Ugandax</i> sp.nov.	X	X	
? <i>Pelorovis</i> sp.		O	
<i>Kobus</i> sp. A	O	X	
" " B	O		
" " C			possibly SH
<i>Praedamalis deturi</i>		O	
? <i>Damalops</i> sp.	X	X	
Alcelaphini sp. 2	O		
" " 3	O		
<i>Aepyceros</i> sp.	X	X	also BM
<i>Madoqua</i> ? <i>avifluminis</i>			KH
? <i>Raphicerus</i> sp.	O		
? <i>Neotragini</i> sp.indet.			unknown
<i>Gazella</i> sp.		O	
Ovibovini sp.aff. " <i>Bos</i> " <i>makapaani</i>			middle or upper Hadar Formation

(X = abundant, O = less common)

were present but did not include *Connochaetes* or any apparent relatives. Impala, dik-dik, one or more other neotragines, and a gazelle can all be found at the present day although the impala does not now occur so far north. The ovibovines are extinct in Africa, probably since the early Pleistocene. The list does not show a preponderance of Alcelaphini (other than *Aepyceros*) as at Olduvai Gorge, or of Tragelaphini, Reduncini and *Aepyceros* as in the Shungura Formation. The common ?*Damalops* and rarer neotragines and gazelle suggest open or fairly dry conditions, while the bovine, reduncine, and *Aepyceros* suggest that water was available and scrub was present.

It is possible to analyze the bovids at a finer subdivision of the stratigraphic levels, as has been done in outline for the whole fauna by Johanson et al. (1978:557) who make the interim suggestion of three faunal units: a lower in SH-1 and 2, a middle in upper DD-1 and 2, and an upper in DD-3 and KH-1. Most fossils of the lower unit come from near the base of SH-2. Table 2 shows the distribution of bovids in more detail, and one can deduce from it the degree of support given by bovids for the suggested faunal units. The few bovid remains in SH-1 and below are nearly all *Aepyceros*. In SH-2 there is ?*Tragelaphus* sp. nov., *Ugandax*, ?*Damalops*, and much *Aepyceros*. SH-3 has few remains but reduncines make their first appearance here. SH-4 to DD-1 are practically barren of bovids. DD-2, containing the middle faunal unit, has the most abundant bovid fauna; common elements are *Tragelaphus* aff. *nakuae*, *Ugandax*, *Kobus*, ?*Damalops*, and *Aepyceros*. More than a third of the identified bovids at this level belong to *Kobus*. In DD-3, with the upper faunal unit, the proportion of *Kobus* and *Aepyceros* appears to drop and ?*Damalops* to increase.

The evidence of the Hadar Formation bovids for faunal correlations with other sites can be summarized as follows:

Tragelaphus aff. *nakuae* of DD appears to date from before Shungura C-D.

The absence of a boselaphine suggests a later age than Langebaanweg E Quarry or Lothagam Member 1.

Ugandax of SH and DD fits an age no later than Shungura upper B and probably earlier.

The main *Kobus* species found in DD is similar to but not conspecific with a species in Shungura upper Member B. The interesting conformation of the reduncine P₄ at Hadar is not known at all from the Shungura Formation or from Pleistocene and Recent reduncines. Either it is a local development or it indicates an earlier level of reduncine evolution.

Praedamalis deturi from DD is also found in the Laetoli Beds, Laetoli.

TABLE 2
Distribution of Bovids of the Hadar Formation

	BM	SHT	SH-1	SH-2	SH-3	DD-1	DD-2	DD-3	KHT	KH-3	Level unknown
<i>Tragelaphus</i> aff. <i>nakuae</i>							X	X			
? <i>Tragelaphus</i> sp. nov.				X							
<i>Ugandax</i> sp. nov.			O	X	O	O	X	X			
? <i>Pelorovis</i> sp.							O				
<i>Kobus</i> sp. A					O		X	X			
<i>Kobus</i> sp. B					O						
<i>Kobus</i> sp. C											O
<i>Praedamalis deturi</i>							?	O			
? <i>Damalops</i> sp.			O	X	X		X	X		O	
Alcelaphini sp. 2				O							
Alcelaphini sp. 3					O						
<i>Aepyceros</i> sp.	O	O	X	X	O	O	X	O			
<i>Madoqua</i> ? <i>avifluminis</i>									O		
? <i>Raphicerus</i> sp.			O				O	O			
? <i>Neotragini</i> sp. indet.											O
<i>Gazella</i> sp.			O				O				
Ovibovini sp.											O

(X = 5 or more specimens, O = less than 5 specimens)

?*Damalops* from SH and DD is not related to the well-known Pliocene and Pleistocene *Parmularius*. Its primitive characters suggest an age well before Olduvai Bed I. It has some likeness to alcelaphines from the Pinjor Formation and from an unknown horizon at Laetoli.

Aepyceros horn cores suggest that the Hadar Formation as high as DD predates upper Member B of the Shungura Formation, but their temporal relationship to those of the Mursi Formation is not clear. The latter look advanced in having more curvature but they also have weaker transverse ridges. This combination warns against taking too simple a view of character changes in space and time.

A neotragine horn core from KHT is like horn cores from the Ndolanya Beds at Laetoli.

Radiometric and palaeomagnetic dating suggest an equivalence in age between the Hadar Formation and Members C and upper B of the Shungura Formation. It is therefore interesting that among the bovids *Tragelaphus* aff. *naku*ae, *Ugandax* and *Aepyceros* of the Hadar Formation look more primitive, and by implication, earlier than their counterparts in Shungura C, C, and upper B respectively. Reduncine P₄s are also not the same as in the Shungura Formation, and they are probably at an earlier evolutionary level. While it is conceivable that contemporaneous species could differ in characters that cause one to look more primitive than another, it is noteworthy that it is always the Hadar form which looks primitive. Moreover, the only other Hadar bovid to offer a clue for faunal correlation is *Praedamalis deturi*, which again suggests an older age than Shungura upper Member B.

The Amado bovids give the impression of being Pliocene or older with the archaic-looking *Tragelaphus*, *Kobus porrecticornis*, and *Gazella jansenschi*, and with the low crowned teeth of the bovine and *Aepyceros*. The large size of the *Aepyceros* horn cores goes against this judgment, however. The Geraru bovids offer fewer clues about age but could be younger than the Hadar Formation since *Tragelaphus naku*ae and *Syncerus* are present.

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